SOME NEW CASES OF MENDELIAN INHERITANCE

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(WITH FOUR FIGURES)

In crosses between nearly related elementary forms, numerous investigations have shown that a very wide range of characteristics in a great many species of both plants and animals behave in the Mendelian way; that is, they give a uniform progeny in the first hybrid generation (F_1), and show perfect segregation of the various characteristics in F_2 and later generations. So consistent have been the results that there can be no question that MENDEL'S law has fundamental and widespread applicability, but it has also been demonstrated that it has its limitations. Where these limitations lie and why it is thus limited may not be known until a much larger mass of data is on record than is now available.

Several of the cultures at the Station for Experimental Evolution, upon which no report has yet been published, present new instances of Mendelian heredity under conditions which make their consideration desirable, even though only a preliminary account can be given at this time.

HELIANTHUS ANNUUS L.

Among 112 plants of the so-called "Russian" sunflower (*Helianthus annuus* var.) grown at the Station during the summer of 1904, all but one had the usually unbranched stem surmounted by a single large head. Sometimes these had several weak branches in the axils of several of the lower leaves, but there were never more than three or four of these lateral branches, and none ever stood higher on the stem than the fifth node above the cotyledons. The one exceptional individual had strong branches in nearly all of the axils and bore a number of somewhat smaller heads, but was not observed to differ in other respects from its unbranched neighbors (*figs. 1, 2*). The seeds had been purchased at a seed store, and nothing is known of the antecedents of these plants.

Not until late in the season was it decided to investigate the hereditary qualities of the branching habit, and consequently the pollination was not guarded. Attempts at getting self-fertilized seeds from other plants proved unsuccessful, however, and all my experience in breeding the sunflowers during the past four years indicates that they are entirely self-sterile. From this it may be safely inferred that the

FIG. 1.—"Russian" sunflower (*Helianthus annuus* var. hort.) showing two pure-bred strains; unbranched on the left, branched on the right.

branched individual (pedigree no. 04109) was cross-fertilized; and as it was the only individual of its kind, it must have been fertilized by means of pollen from the unbranched individuals. Assuming that this branching habit is a Mendelian character, several possible assumptions would lead to different expectations regarding the offspring of this cross: (*a*) If the unbranched habit were dominant over the branched, all the offspring should be unbranched; (*b*) If the branching habit were dominant, there would be two cases: (1) when the branched parent is a pure dominant, the offspring should be all branched; and (2) when the branched parent is a heterozygote (DR), the offspring should consist of both branched and unbranched individuals in the ratio 1:1.

In the summer of 1905, 59 offspring were reared from this cross, 28 branched and 31 unbranched, showing either that branching is

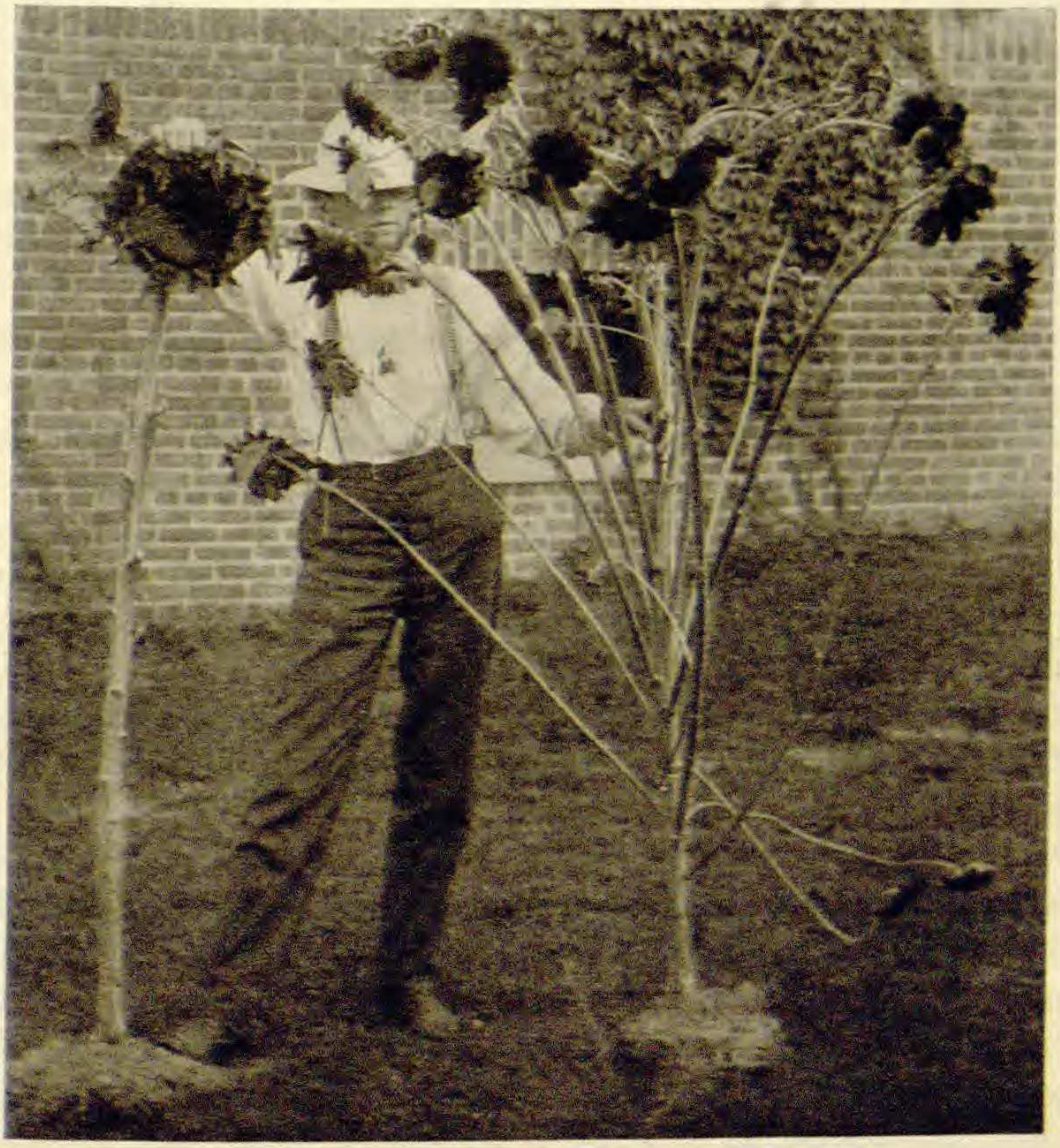

FIG. 2.—Individuals representing two elementary strains of the "Russian" sunflower; leaves removed to display the branching habit.

dominant, and the original branched plant was a heterozygote, or that branching is not a Mendelian character. About half of the unbranched plants showed a few weak branches about the base, but none had more than four branches, while none of the branched individuals had less than nine branches, the average number of branches in the latter being about 15.

During the same season, 81 offspring of an unbranched plant (04108) which had also been left unguarded showed 72 unbranched and 9 branched. This result would find a ready explanation in case branching is a Mendelian unit-character, simply as the usual result of vicinism. On this assumption the proportion of branched offspring in this family indicates that the pistil-parent (04108) received about one-fifth of its fertilizations from the branched specimen (04109) which was growing near it, and the other four-fifths from the 110 unbranched plants, several of which were growing equally near.

In 1906 the Helianthus cultures were started several weeks too early (April 2) and became tall and slender from long crowding and insufficient illumination before they could be set into the garden. Some of these began to bloom shortly after they were transplanted, and the branching habit was very much deranged. Two families, (05149 and 05150) raised from branched parents having had the pollination fully controlled, resulted in 54 branched and 2 nearly unbranched in the one case, and 68 branched and 2 unbranched in the other, but as the whole branching system was considerably modified the classification could not be made with security. The expectation in these cases, since both parents were DR, would have been branched and unbranched approaching the ratio 3:1. The results secured indicate either that we are not dealing with a Mendelian character or that the conditions of the culture caused an excessive development of branches in normally unbranched individuals. The latter suggestion is strengthened by a small family (05145) reared from fully guarded unbranched parents from the same hybrid family to which the branched parents of the last-mentioned two families belonged. Both parents should be in this case extracted recessives (RR), and all of the offspring should belong to the unbranched class. Only six offspring were produced, and all showed some branching, ranging from one strong branch below the middle to twelve branches from the middle to the top of the stem, the latter type of branching being characteristic of the branched form. The results in 1906 seem therefore to oppose distinctly the idea that the branching character is Mendelian, but still leave a doubt on account of the obvious derangement produced by ill-treatment.

In the summer of 1907 the seeds were sown at the proper time (April 30) and the Mendelian character of the branching habit was fully established by the following facts: (*a*) Reciprocal crosses (06356 and 06357), fully controlled, between two strongly branched specimens belonging to the second of the two DR families mentioned in 1906 (namely, no. 05150) gave 65 fully branched individuals in the one family, 13 in the other family, and no unbranched specimens in either, thus showing that at least one of the chosen parents was an extracted dominant (DD). The number of branches in both these reciprocal families ranged from 10 to 25. (*b*) Properly controlled pollinations were made between two specimens of the last family (05145) mentioned for 1906, supposedly a recessive family. The pistil-parent had two strong branches, one of which showed an abnormal bifission. The pollen-parent had one strong lateral branch which exceeded the main stem. The cross was made between two heads borne by lateral branches. Of the 22 offspring produced (06353), 19 were wholly unbranched, two had one small branch, each near the base of the stem, and one had two small branches similarly located. This demonstrated that both parents were pure recessives and showed that the branches produced the preceding year had no hereditary significance. (*c*) Another sowing (06352) was made of unguarded seed from the same pistil-parent as the last. The 91 offspring consisted of 67 individuals having less than 7 branches each and 24 having more than 7 branches each, the latter group having an average of about 16 branches and the former group an average of less than two branches (*fig. 3*). As the branched type does not usually have more than 4 or 5 vacant axils above the highest branch, one individual having 8 branches and 10 vacant axils probably belongs with the unbranched class. The result in this family shows that about one-fourth of the pollen received by the unguarded mother came from branched individuals, and as this fact was made obvious in the first generation it gives further proof of the dominance of the branching habit over the unbranched.

Furthermore, it illustrates well how impossible it would be to discover Mendelian ratios in cross-fertilizing species or varieties without careful control of fertilization. This requirement accounts for two things, namely, the fact that MENDEL'S law was not discovered by economic plant-breeders and gardeners long ago, and that in certain quarters the notion prevails that Mendelian inheritance is a function only of self-fertilizing or inbred strains.

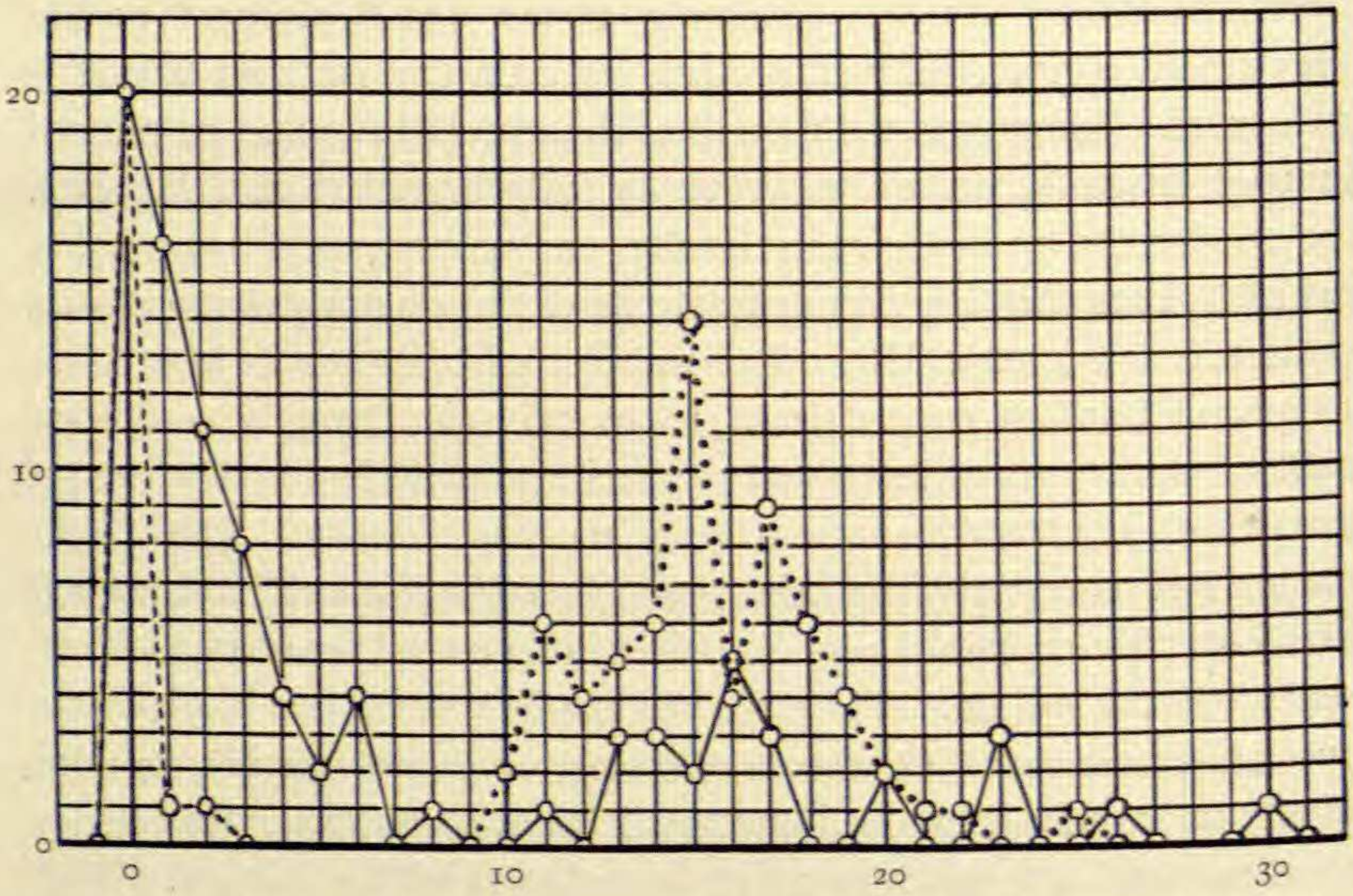

FIG. 3.—Curves showing the extent of branching in three families of "Russian" sunflower; the dotted line at left represents the offspring of two unbranched parents; the dotted line at the center represents the offspring of two branched parents, one of which must have been an extracted dominant; the unbroken line shows the condition of a family from the mother of the pure unbranched family, but with pollination unguarded; the dominance of branching produces a branched offspring in each case that successful fertilization took place by means of pollen from a branched plant.

The foregoing account of experiments on the inheritance of the branching habit in *Helianthus annuus* may be recapitulated in the form of a family tree thus:

Branched (DR) × Unbranched (R)

28 B (DR) 31 U (RR

{ 54 B(DD+DR+RR 2 U (RR }
{ 68 B DD+DR+RR 2 U (RR }

6 RR)
More or less branched

{ 65 B DD or DR) }
{ 13 B DD or DR) }

22 U RR

During the summer of 1905 experiments were also begun for the purpose of testing the relationship between the Russian sunflower and the wild *Helianthus annuus* of the prairie region. Seed of the latter had been received from Nebraska through the kindness of Dr. C. E. BESSEY. Several points of contrast were noted between the plants produced from this seed and the Russian sunflower, the most noteworthy being with regard to branching habit and the color of the disk. The lower branches of the wild sunflower, when given space for full individual expression as they are in my cultures, diverge almost horizontally, having on this account a slightly wider spread than branches arising at higher points on the stem. At the time the first head is ready to spread its rays, the whole plant has a nearly conical form. The development of the primary head checks the growth of the main stem, and some of the upper branches then usually elongate so as to overtop the central axis, thus giving the mature plant a more columnar form. My branched type of the Russian sunflower has all the branches strongly ascending, the lower being enough longer than the upper to reach almost the same level, thus giving the mature plant a corymbose or broadly obconical form.

I have not yet reached a conclusion in regard to the hereditary behavior of these two types of branching, as it is not easy to find decisive criteria for the exact classification of the two forms and their combinations. It has been apparent, however, in my cultures that there is a combination of both types of branching in many if not all of the first-generation hybrids, and at least some segregation in the next generation. The indefiniteness of the character will probably make it difficult to reach satisfactory quantitative results, but the attempt is being made.

A very much simpler character to deal with is the color of the disk. All of the western *Helianthus annuus* that I have thus far observed have a deep purple disk, the color being found in the tips of the paleae, which are of a deep, metallic purple; the margin of the corolla, which is brownish purple; and the style and stigmas, which are reddish purple. In all my Russian sunflowers, the tips of the paleae are yellowish green, the corolla is a clear lemon yellow, and the styles and stigmas usually have the same color as the corolla; but in a small proportion the stigmas are margined with a narrow line of deep crimson, which gives the stigmas the appearance of being orange colored, unless examined closely. No study has been made of the inheritance of this stigmatal margin, but it seems not unlikely that it too may prove to be a Mendelian character. Although the color of the disk affects several organs of very different morphological value, it proves to be a simple character, showing the same kind of correlation that is found in peas and beans which have purple flowers and black seeds, and other plants which have purple flowers associated with more or less purple in the stems.

The cross made during the summer of 1905 between the purple-disked wild sunflower and the yellow-disked, branched, garden sunflower, produced in 1906 a progeny (05153) consisting of 26 with purple disks and 27 with yellow disks; when I would have expected all purple on the assumption that both parents were pure-bred and purple dominant over non-purple, as has been the general experience with the purple color-character in other plants. The conclusion reached was that either the purple disk is not a Mendelian character or the purple parent was a DR instead of a pure-bred purple. As yellow disks have not appeared among my cultures of wild sunflowers during three years, the assumption that the one plant which I used for the cross was itself a hybrid seemed very unlikely, and the probability that this strictly alternative character was not behaving according to Mendelian expectation led me to watch the culture the following season (1907) with great interest. Five F_2 families were raised, two reciprocal families of purple by purple, representing the hypothetical cross DR×DR; two reciprocal families between purple and yellow, representing the cross DR×R; and one family of yellow by yellow, representing the cross R×R. The results were as follows:

DR×DR	No. 06359,	64 p:21 y
	No. 06360,	64 p:16 y
	Total,	128 p:37 y
	Expected,	123 p:41 y
DR×R	No. 06361,	48 p:46 y
	No. 06362,	39 p:41 y
	Total,	87 p:87 y
	Expected,	87 p:87 y
R×R	No. 06358,	96 y
	Expected,	96 y

From all of these results it must be concluded that the purple disk is a strict Mendelian character, and that the first purple-disked parent was a heterozygote. The original cross is being repeated to make the latter point more certain.

Lychnis dioica L.

This plant is a native of Europe and was doubtless very often cultivated in the gardens of a generation or more ago. It has now commonly escaped from the gardens and is maintaining itself quite generally along roadsides in the eastern United States. The flowers show considerable variation in the intensity of their purple color, and white-flowered ones are quite common. Purple and white flowers have been crossed in so many species and found to follow Mendel's law, that there would have been little incentive to study this particular character in *Lychnis dioica*, had it not been for the fact that this species is dioecious, and that in consequence self-fertilization could not be held responsible for the Mendelian behavior if it should be found to exist. Statements in the manuals regarding the dioecious habit of this species indicate that it also occurs as a hermaphrodite, but among about five thousand individuals which I have examined only one was noted which had both stamens and pistils, and that one had but a single flower with both kinds of sporangia.

During the summer of 1905 I made all possible combinations with white and purple flowers, but in one case unfortunately used two different purple-flowered individuals for the pollination of the same white-flowered plant and collected the seeds from both crosses together. The offspring from these crosses reared in 1906 were as follows:

No. 05212, w × w,	90 w
No. 05213, w × 2 p's,	66 p : 41 w
No. 05114, p × p,	65 p : 23 w
No. 05115, p × p,	96 p

The fact that two white-flowered parents produced nothing but white-flowered offspring, and that in one case two purple-flowered parents produced only purple-flowered young, shows pretty conclusively that we are dealing here with a Mendelian pair of characters, even though the one family (05114), which probably represents the cross DR × DR, shows a considerable departure from the expected ratio of 3p:1w. The ratio of purple to white in family no. 05213 can have no significance, since one of the two purple plants used as the pollen parents was probably a D and the other a DR.

To test the assumption that family no. 05114 represented the cross DR×DR, and to get further evidence on the Mendelian character of the purple color in this species, a series of over eighty crosses was made within this single family. All of the pistillate plants received pollen from a single white staminate plant, and pollen from each of the staminate plants was used to fertilize the different flowers of a single white pistillate plant.

This method was employed because it is the simplest way in which the correct classification of every individual of the first generation of hybrids may be attained. Every single cross in the series had the recessive white as one of its members, so that only three possible combinations could occur among the resultant hybrid families, namely, D×R, DR×R, and R×R, giving respectively, according to expectation, 100 per cent., 50 per cent., and 0 per cent., of purple-flowered offspring, in the ratio 1:2:1. About 50 plants from each of these 83 crosses were reared to maturity in 1907, and, when classified according to the percentage of purple individuals in each family, showed 13 families with more than 95 per cent. purple, 48 having 30–70 per cent. purple, and 22 with less than 5 per cent. purple, the expectation being 21 with 100 per cent. purple, 42 with 50 per cent. purple, and 21 with 0 per cent. purple. The result is close enough to expectation to demonstrate the correctness of the Mendelian law in regard to the flower-color of *Lychnis dioica* L.

The diagram (*fig. 4*) showing the distribution of percentages of purple individuals in the heterozygote families may be used to call attention to what we ought to mean by "Mendelian expectation." Very often when a rather small series of observations shows a considerable departure from the ratios 1:1, 1:2:1, 3:1, 9:3:4, or whatever other ratio represents the theoretical limit appropriate to the conditions of the particular experiment in hand, the statement is made that the results are not in accord with "Mendelian expectation." When the number of observations is small, such a statement is usually due to the fact that too much is expected. This will become clear when attention is called to the fundamental basis of the Mendelian ratios. Equal numbers of both eggs and sperms carry the antagonistic or alternative qualities making up a pair of Mendelian units. These different germ cells unite according to the laws of chance, and we should mean therefore by the expression "Mendelian expectation" that our observations if seriated in the form of a curve will present a normal probability curve within the limits of probable error. Not until the number of observations becomes infinite have we a right to expect absolute agreement with the theoretical ratios.

Analysis of the curve presented by the heterozygote families of *Lychnis dioica*, as represented in the diagram, shows that it approaches closely to the normal probability curve, and that therefore every proper expectation is fulfilled. As the departure of variates from the mean is a fundamental part of the law of chance, the fulfilment of expectation is just as complete in the case of the one DR×R family that had only 35 per cent. of purple-flowered individuals, or the three similar families that had about 65 per cent. of purple flowers, as in the twelve families which consisted of about 50 per cent. purple. This is an important fact that needs to be taken into account by both the student and the critic of Mendelian inheritance.

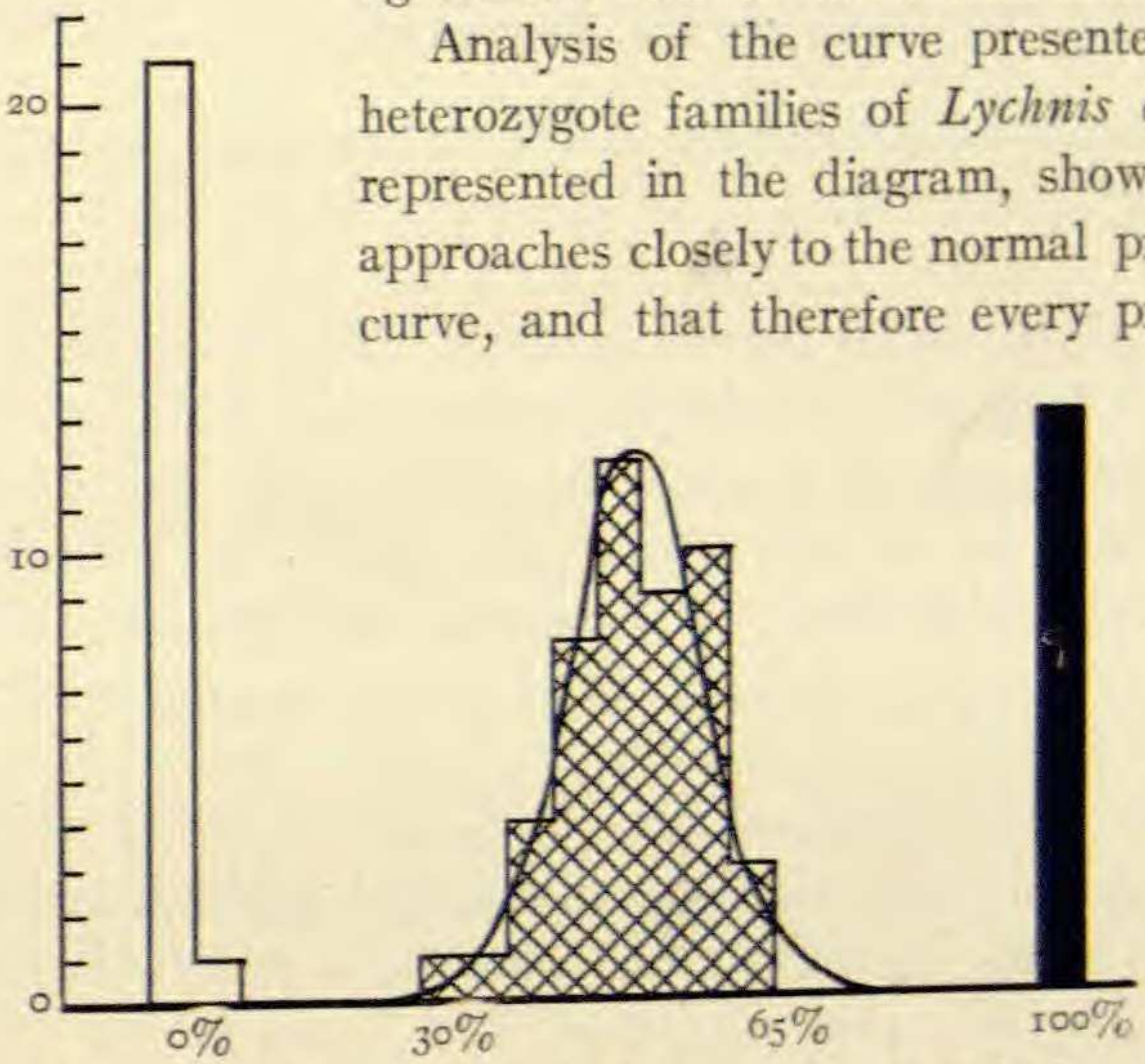

FIG. 4.—*Lychnis dioica* L.: variation in the percentage of purple-flowered offspring in hybrid families of the third generation having the form (D+2DR+R)×R; left-hand group represents the extracted recessives (R×R), the right-hand group the extracted dominants (D×R), and the middle group the heterozygotes (DR×R); superposed upon the heterozygote group is the normal curve having the same standard deviation, showing the close agreement with a perfect chance distribution.

The results here presented both in regard to Lychnis and Helianthus show that Mendelian phenomena stand in no relation to self-fertilization, since neither of these species can self-fertilize. Emphasis upon this point should not be needed, since many of the most typical cases of Mendelian inheritance occur among animals, where the sexes are almost invariably separated.

VERBASCUM BLATTARIA L.

There are two color-varieties of this widely distributed species, one having bright-yellow flowers, and the other having the flowers almost white. If examined carefully, however, the pale flowers are seen to be cream colored rather than pure white. Two considerations made it appear desirable to determine the relation between these two color-varieties by means of crossing. (*a*) Many cases are on record in which albinos are found to be typical Mendelian recessives when paired with certain colors. In *Verbascum Blattaria* the pale flowers approach the albino condition, but both forms possess some color, and it is of interest to know whether this pale-flowered form behaves in the same manner as an albino. (*b*) Several studies in which yellow has been paired with white have shown that yellow is in these cases recessive to white. Thus CORRENS[1] found white *Polemonium coeruleum* dominant over the yellow *P. flavum;* and BATESON[2] has shown that yellow-flowered stocks (Matthiola) are recessive to the white-flowered. CORRENS' results with Polemonium stood alone at the time my experiments with Verbascum were begun, as an instance in which a white-flowered variety dominated one with colored flowers. It seemed important on this account, also, to know what would be the behavior of the yellow-flowered *Verbascum Blattaria* when crossed with its pale-flowered form.

To secure a solution to these problems, several crosses were made during the summer of 1904. The seeds were sown in the spring of

[1] CORRENS, C., Weitere Beiträge zur Kenntnis der dominierenden Merkmale und der Mosaikbildung der Bastarde. Ber. Deutsch. Bot. Gesells. 21:195–201. 1903. (See p. 198.)

[2] BATESON, W., SAUNDERS, Miss E. R., and PUNNETT, R. C., Reports to the Evolution Committee of the Royal Society, II. 1905, and III. 1906.

1905, but the plants did not bloom until the summer of 1906. The results then stood as follows:

No. 0446,	y × y,	75(?) y
No. 0447,	w × w,	53 w
No. 0448 × 47,	w × y,	8 y
No. 0448 × self,	y × y,	(?) y (number unrecorded)

Among the members of these families all possible combinations were again made. The offspring of these crosses were mostly induced to bloom the first season by starting early and giving the seedlings the best possible conditions. The results of the second generation were thus secured during the summer of 1907, and showed the following composition:

No. 06241,	D × R,	26 y
	Expected,	26 y
No. 06244,	DR × DR,	5 y: 7 w
	Expected,	9 y: 3 w
No. 06243,	R × DR,	13 y: 18 w
No. 06245,	DR × R,	5 y: 8 w
	Total,	18 y: 26 w
	Expected,	22 y: 22 w
No. 06242,	R × R,	90 w
	Expected,	90 w

Although some of these ratios depart rather strongly from the theoretical limiting ratio, this is due entirely to the small numbers of observations, as pointed out above in the discussion of Lychnis. It is plain therefore that the color-forms of *Verbascum Blattaria* constitute a Mendelian pair, and that the bright yellow is dominant over the pale. The dominance of yellow in this cross is just the reverse of the behavior of yellow in Polemonium and Matthiola, and teaches that there are two kinds of yellows in plants, one of which is dominant to white, the other recessive to white. A microscopic examination of the petals of Verbascum shows that BATESON'S[3] distinction between plastid-colors and sap-colors is probably fundamental, as the yellow color in this species proves to be a sap-color, and its behavior in combinations with white is the same as that of the blue, purple, and red

[3] Loc. cit.

sap-colors; while the yellow color of Matthiola and of *Polemonium flavum* are plastid-colors and this must account for their different behavior. In Mirabilis CORRENS[4] has noted a yellow-flowered variety, *M. Jalapa gilva*, in which the yellow color seems to be dominant. I do not know that any examination has been made to determine the basis of the yellow color in Mirabilis, but I predict that it will be found to be a sap-color. HURST[5] reports, on the contrary, that the yellow of *Antirrhinum majus*, which is recessive to white, is a sap-color. If this statement is correct, this species seems to stand alone at present in the possession of a sap-color recessive to white. Why a plastid-color should be recessive to the absence of that color calls for an explanation which science is not yet ready to give. This difference between the two kinds of yellow recalls a similar situation in poultry, in which white is usually dominant over colors, but in at least one strain (Silky) the white is recessive.

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[4] CORRENS, C., Zur Kenntnis der scheinbar neuen Merkmale der Bastarde. Ber. Deutsch. Bot. Gesells. **23**:70–85. 1905.

[5] HURST, C. C., Mendelian characters in plants and animals. Rep. 3d Internat. Conference on Genetics, 1906. Roy. Hort. Soc. **1907**:114–128. *figs. 6.*